Reference: *Biol. Bull.*, **139**: 495–501. (December, 1970)

SENSITIVITY OF ECHOLOCATION IN CAVE SWIFTLETS

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The specializations of bats of the suborder Microchiroptera for echolocation have naturally suggested that nocturnal or cave dwelling birds might orient themselves in the same way. Numerous preliminary tests of several species (mostly unpublished) have yielded negative results, and only two avian genera have been clearly demonstrated to use echolocation. These are the oilbirds of South America, *Steatornis caripensis* (Griffin, 1954), and certain species of the genus *Collocalia*, the cave swiftlets of Southeast Asia (Griffin, 1958; Novick, 1959; Medway, 1959, 1967). The orientation sounds of both species are brief audible clicks lasting a few milliseconds. They tend to have a peak of energy between two and eight kHz, but also a very broad acoustic spectrum extending to ultrasonic frequencies. The clicks are emitted primarily in dim light or darkness and increase in repetition rate like those of bats and cetaceans when difficult orientation problems arise. A very similar sort of echolocation is practiced by bats of the genus *Rousettus*, the only known case in the suborder Megachiroptera.

Although oilbirds and swiftlets can certainly avoid large obstacles by echolocation, there is very little evidence concerning their proficiency, and we know almost nothing about the minimum size of object that can be detected. In contrast considerable data on this point are available from bats of the suborder Microchiroptera (Griffin, 1958; Suthers, 1965, 1967; Schnitzler, 1966). Griffin, Novick, and Kornfield (1958) measured the size of cylindrical obstacles that could be detected by a single individual *Rousettus aegypticus*. With sufficient practice this animal could detect wires as small as 0.46 millimeter diameter at distinctly above the chance level. *Rousettus* uses as orientation sounds audible clicks that are similar to those of *Collocalia* and *Steatornis*, but in view of evidence that most small mammals can hear well at ultrasonic frequencies (Ralls, 1965) it is difficult to ascertain which part of the broad frequency spectrum emitted by *Rousettus* generates the echoes by which it detects small obstacles. Medway (1967) studied the ability of *Collocalia fuciphaga* to avoid vertical wooden rods one centimeter square spaced 15 cm apart. These birds with a wingspan of about 27 cm showed no ability to avoid these obstacles when first encountered in darkness. But they maneuvered between them almost perfectly in the light. Their performance in the dark improved on successive flights, but the experiment did not demonstrate how much of this improvement resulted from learning the positions of the obstacles and how much from echolocation. The many species of *Collocalia* appear to differ widely in their use of dark caves and their reliance on echolocation.

During the 1969 Alpha Helix expedition to New Guinea we studied the orientation sounds of *Collocalia vanikorensis granti*, and carried out preliminary experiments that indicate the approximate threshold size of cylindrical obstacles detectable by echolocation. This species nests in a totally dark chamber of a cave near Amele, south of Madang, which we visited twice in June, 1969, for preliminary observations. Local opposition of a quasi-religious nature prevented extensive studies of this colony, but through the kindness of Dr. Kiro Kikkawa three birds of the same species were obtained in mist-netting operations near Omuru within a few km of this cave.

METHODS

The obstacle avoidance tests were conducted in a dark chamber constructed from a double layer of heavy, opaque, black plastic. This was shaded and sheltered from rain by a fly of the same material below a thatched roof. A small air conditioner was used to maintain a temperature of approximately 26–28° C. The tests were conducted both in the daytime and after dark, but the chamber was sufficiently light-tight that even in bright sunlight, and when we were fully dark adapted, we could not see large white objects. All test obstacles were small wires or rods extending vertically from floor to ceiling and spaced 40 cm apart horizontally. With the lights off they were quite invisible. The chamber was 4.9 meters long, 2.9 meters wide and 2.1 meters high with its long axis approximately east-west. Near the center, 2.3 meters from the west end, a wooden frame around the walls, floor, and ceiling reduced the height to 1.86 meters. On this frame we mounted a series of cords and pulleys from which obstacles were mounted and shifted horizontally in position while maintaining their horizontal spacing. The obstacles mounted on this frame will be referred to below as the middle obstacles. Three additional rows of vertical obstacles were hung from hooks in the ceiling at 1.5, 2.4, and 3.9 meters from the west end of the chamber. These could also be shifted between the fixed positions of hooks in the ceiling, but this type of shifting was less convenient and was carried out less often. The obstacles in the middle plane were fastened by rubber bands at their tops and bottoms while those in the other three rows were held straight by light weights. The swiftlets almost always flew at least 30 cm below the ceiling and at an even greater distance above the floor, both in the light —where they could easily be seen—and in darkness where we could locate them by their audible orientation sounds. All trials considered below consisted of flights through the obstacle planes at 30 cm or more from walls, or ceiling. The smallest obstacles tested were supported by attachments of the same size as the larger obstacles. In view of the poor performance with the smallest obstacles tested we did not take stringent precautions against the possibility that the echolocation achieved by these birds was based on echoes from the weights stretching the obstacles at the bottoms of three rows, or the attachments of the ceiling.

Cave swiftlets are delicate birds which are difficult to maintain in captivity in good physical condition for more than a day or two, even though they were force-fed food mixtures suitable for insectivorous birds. All experiments considered below involved swiftlets that had been in captivity only one or two days and appeared approximately as vigorous and adept at avoiding obstacles as when first brought into the flight chamber. All data from these four birds during this period are included in Table I except for times when they would, after several minutes of flight, temporarily appear weak or refuse to fly the length of the flight chamber. One of us held each bird in the hand roughly 30–40 cm below the ceiling and released it only after the lights were extinguished. In most cases one of us watched with the infrared viewer from the opposite end of the flight chamber in the hope of observing the bird's flight path. This instrument afforded a clear view of the moving bird in only a minority of the flights, but careful listening to the orientation sounds sufficed to show the bird's approximate flight path, and as soon as it had passed through one to four barrier planes we switched on our flashlights and inspected the obstacles immediately to detect vibration or other motion. Unfortunately the sound of contact with obstacles could not be used, as we have commonly done with bats, because it was masked by the orientation sounds of the birds. Since no test was begun until all obstacles had again come to rest, and since even a light brush of a swiftlet's wing set the obstacles in evident motion, we feel confident that we detected most contacts with obstacles.

TABLE I

Obstacle avoidance scores of Collocalia vanikorensis granti *flying through an array of vertical wires and rods. N indicates number of trials, % M per cent misses. All flights in darkness or with the bird blindfolded. The flights marked "Shifted" were those immediately after the obstacles had been moved horizontally by several centimeters.*

Bird No.	Date	2 mm plastic covered wires		6.3 mm iron rods		8 mm plastic tubing	
		N	% *M*	*N*	% *M*	*N*	% *M*
1	23 July	20	50%				
	23 July (blindfolded)	56	46%			16	63%
2	23 July	82	48%			20	80%
	24 July	26	42%	17	76%	20	70%
3	25 July	55	31%	31	74%	31	58%
4	29 July	68	40%	29	83%	30	77%
	29 July (shifted)	2	50%	12	92%	10	70%
Total July 24–29		151	37%	89	80%	91	68%
Total of all birds		309	43%	89	80%	127	68%

The positions of the obstacles, particularly those in the middle row, were shifted horizontally from time to time without any noticeable effect on the birds' success at avoiding them. An especial effort was made to do this with bird No. 4. It was enclosed in the cupped hands while obstacles were shifted and released only after the lights had been turned off. The performance of this bird was somewhat better during flights immediately after such a shift in obstacle position. It thus seems unlikely that learning of the position of obstacles (Griffin, 1958, pp. 162–167; Neuweiler and Moehres, 1967) had any appreciable effect in these experiments. The two millimeter obstacles were shifted less often than the larger ones, so that the birds had a better opportunity to learn their positions, but this did not eliminate the substantial difference in avoidance of the larger and smaller cylinders.

The orientation sounds of two swiftlets were recorded as they flew in the darkened chamber with a Roberts model 6000 stereo tape recorder and Electro Voice model 644 microphones. The frequency response of this system was limited by the microphone which was flat within about ±3 dB from 700 to 12,000 Hz and down about 10 dB at 17,000 Hz. Portions of this recording were displayed on an oscilloscope and photographed for further analysis. Spectrographs of a number of clicks were also made with a Kay Electric Co. model 6061B sound spectrograph.

RESULTS

Obstacle avoidance scores for all four birds under all conditions tested are included in Table I for the sake of completeness, but there do not seem to be any significant differences between birds or conditions. Consequently the overall averages provide the most reliable picture. All data are pooled as in the final line of the table, but the last three days are also listed separately because on those days all three birds were tested with all sizes of obstacle. The results are consistent in showing a large difference between 2 millimeter and 6.3 millimeter obstacles and a somewhat poorer performance with the 8 millimeter plastic tubing. The flight paths of these birds were too variable and insufficiently well observed to allow any accurate calculation of chance scores, but the poorest performers registered about 30 to 40% misses. When we watched the birds with the infrared viewer our impression was that the two larger sizes of obstacles were avoided by turns and dodging maneuvers. But the resolution of this instrument under the conditions of our experiments was too poor to justify much confidence in this observation.

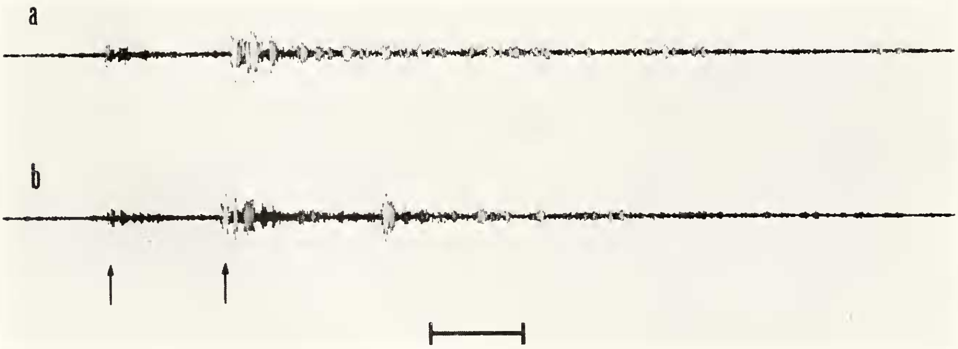

FIGURE 1. Oscillographic display of clicks emitted by *Collocalia vanikorensis;* (a) most commonly emitted type consisting of double click; (b) less common type composed of three high amplitude portions. Arrows indicate two initial high amplitude portions of envelope which are responsible for double vertical bars on sonagrams in Figure 2a. Bar equals 10 msec.

The poorer performance with 8 millimeter plastic tubing than with 6.3 millimeter iron rods is somewhat puzzling, since the echoes from the larger cylinders must have been more intense. Our impression was that motion of the iron rods after a light touch was more difficult to observe and more quickly damped out. Thus we feel the most likely explanation for the drop from 80 to 68% misses was that we failed to detect motion of the 6.3 mm rods after some light touches.

Each orientation sound typically consisted of a moderate amplitude peak a few milliseconds long, followed after several milliseconds by an appreciably higher intensity peak about 4 to 8 msec in duration (Fig. 1a). This second high amplitude peak continued as a gradually attenuated complex waveform which disappeared into the noise level of the recording after about 30 to 50 msec. Much of this terminal portion was probably due to echoes from the chamber walls, floor or ceiling. The double nature of each click was clearly audible when the tape recording was reproduced at one-eighth its original speed. Occasional pulses also showed a third high amplitude peak (Fig. 1b). Click intervals (measured as the time between the maximum amplitude portions of successive clicks, rather than the silent intervals between them) for 477 clicks comprising several flights averaged

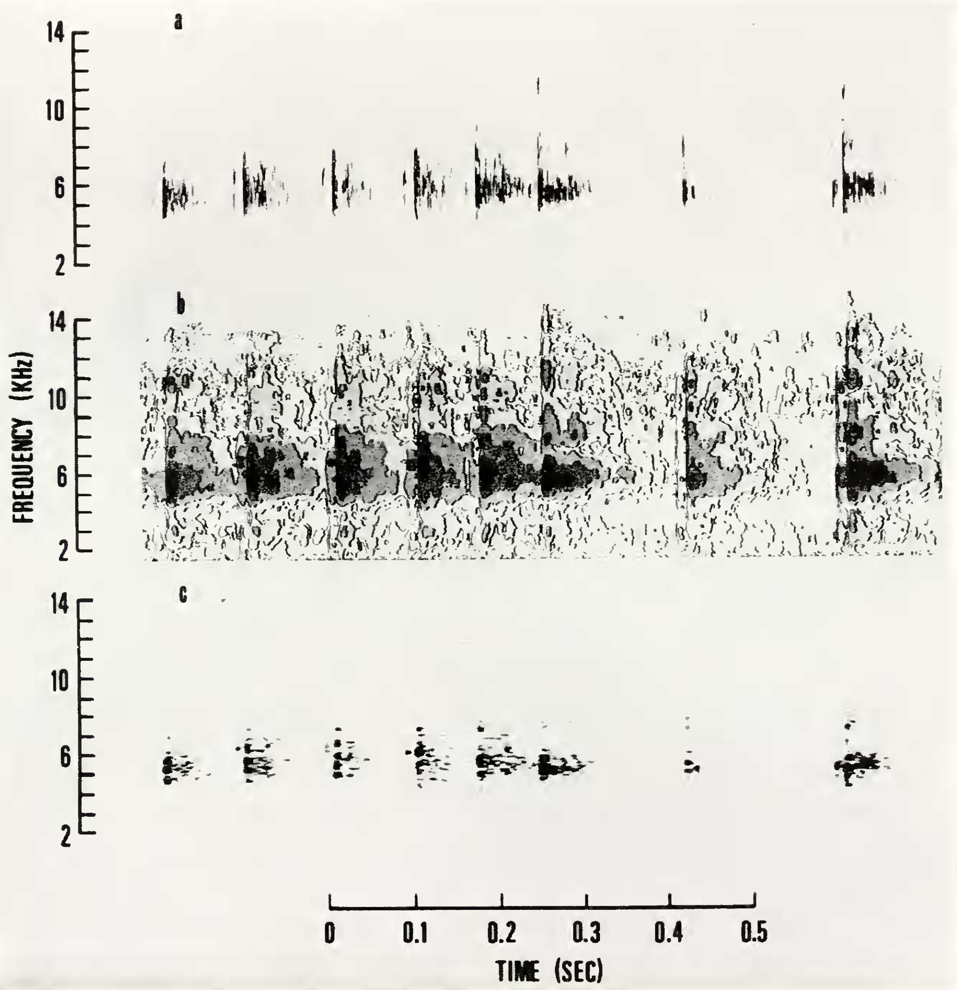

FIGURE 2. Sound spectrographs of eight successive orientation clicks of a single *C. vanikorensis* flying in the dark. Approximate sensitivity of recording system uniform within ±3 dB from 0.7 to 12 kHz and down 10 dB at 17 kHz; (a) wide band width display (300 cps at 3 dB down) showing temporal relationships; (b) intensity contour plot indicating relative intensity by 6 dB steps between contours. Darkest contours represent most intense sounds; (c) narrow band width display (45 cps at 3 dB down) giving better frequency resolution but blurring temporal relationships and losing some lower intensity portions.

116 msec with a minimum of 48 msec and a maximum of 358 msec, corresponding to repetition rates of about 3 and 20 clicks per second, respectively.

The double nature of the clicks is readily visible in the spectrograms (Fig. 2) which also indicate the distribution of sound energy in each click. It is evident that clicks of *C. vanikorensis* have a wide frequency spectrum most of which appears to lie within the human audible range. The highest intensity sound occurs between 4.5 and 7.5 kHz, but as in all impulsive clicks there is appreciable sound energy at higher frequencies. A few clicks showed small amounts of acoustic energy as high as 16 kHz, the upper frequency limit of the spectrogram, but this is uncommon. Very faint low frequency portions of the clicks extend downward to about 2 kHz.

Discussion

Medway (1959) reported most of the acoustic energy of clicks emitted by *Collocalia maxima lowi* occurred between 2 and 4.5 kHz with very little energy below 1.5 or above 5.5 kHz. Novick (1959) found the principal frequency of *Collocalia brevirostris unicolor* to lie between 4 and 5 kHz but noted many overtones. These apparent interspecific differences may in part reflect different sensitivities of the various tape recorders and microphones to high frequencies. It does however appear that clicks produced by *C. vanikorensis* contain relatively more high frequency components than do those of other *Collocalia* thus far studied. The presence of these high frequencies could theoretically improve the bird's ability to detect echoes from small objects. It is interesting to note that Medway (1967) found *C. fuciphaga*, which emits clicks with frequencies principally in the range between 1.5 and 4.5 kHz, unable to echolocate a barrier of wooden rods 1 cm^2 in cross section, whereas our data indicate *C. vanikorensis* regularly echolocates iron rods 6.3 mm in diameter.

While it would clearly be desirable to obtain considerably more extensive data involving more birds, a wider range of obstacle sizes and spacings, and more trials, these results are of interest because no previous investigations have included even such approximate determinations of the threshold sizes of obstacles which *Collocalia* can detect by echolocation. Under more or less favorable conditions the threshold size of obstacles may vary to some extent, but it seems unlikely that it would be far outside the interval between 2 and 6 millimeter diameter cylindrical obstacles.

Although the auditory sensitivity of *Collocalia* has not been studied directly, the extensive data on other birds (Schwartzkopff, 1968; Konishi, 1969) suggest that they are not likely to have high auditory sensitivity extending above 20 kHz. In the absence of direct evidence, it seems most likely that *Collocalia*, like all other birds that have been adequately studied, have a frequency range of hearing roughly comparable to our own. It also seems likely, though not absolutely certain, that *C. vanikorensis* employs orientation sounds without useful components above the range of human hearing. If so, the wavelengths of sound used by these birds for echolocation are also available to blind men attempting echolocation based on audible sounds. This implication of the still very poorly understood acuity of echolocation in *Collocalia* justifies further and more intensive study of the questions discussed in this paper.

The support of the National Science Foundation is gratefully acknowledged, including both the 1969 ALPHA HELIX Expedition, and grant GB 7155 to the New York Zoological Society.

SUMMARY

The acuity of echolocation in *Collocalia vanikorensis granti* was studied by measuring the success of freshly captured birds in avoiding cylindrical obstacles in total darkness. The percentage of misses varied from approximately 40% with 2 millimeter insulated wires to 80% with 6.3 millimeter iron rods and 68% with 8 millimeter plastic tubing. The orientation sounds used for echolocation are clicks with the major energy between 4.5 and 7.5 kHz. Although the frequency range of hearing in these birds has not yet been measured, it seems probable that they can echolocate obstacles as small as 6 millimeter diameter rods by means of frequencies within the range of human hearing.

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